

Effects of temperature rise and water-table-level drawdown on greenhouse gas fluxes of boreal sedge fens

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As potential outcomes of climate change, we examined the effects of environmental warming and drying on instantaneous CO₂, CH₄ and N₂O fluxes in three sedge fens situated in the northern and middle boreal zones. Warming was induced by means of open top chambers (OTCs) and drying through drainage via ditching. OTCs raised the air temperature by 0.2–2 °C, whereas short-term drainage dropped the water-table level (WTL) by 5–10 cm and long-term drainage by 10–30 cm. The impact of simulated warming was rather negligible as warmer and drier conditions caused net ecosystem exchange (NEE) to decrease only at one of the two mid-boreal sites. Otherwise, the temperature rise alone or paired with WTL drawdown did not alter gas fluxes at any of the sites. Instead, the drainage effect overrode that of warming. Primarily WTL drawdown accounted for the differences in fluxes detected, but this was more apparent at the mid-boreal sites than our northern-boreal one. Notably, the northernmost Lompolojänkki sedge fen, which was both the coolest and wettest of the three sites, was least sensitive to temperature rise and drainage; there, only CH₄ emissions were affected by WTL drawdown.

Introduction

Biological activity in boreal mires is currently restricted by low seasonal temperatures and high water-table levels, thus being highly sensitive to changes in climate (Gorham 1991). Globally, boreal mires comprise over half of the total peatland area (Joosten and Clarke 2002), containing almost 60% of all carbon stored in mires (Sampson *et al.* 1993) and even one-third of the total global soil carbon store, i.e., 270–455 Pg (1 Pg = 10¹⁵ g) (Gorham 1991, Turunen

et al. 2002), which constitutes 34%–46% of the amount of CO₂ present in the atmosphere (IPCC 2007). Therefore, disturbance to carbon cycling in boreal mires may markedly affect the atmospheric carbon dioxide (CO₂) concentration, consequently acting as a positive or negative feedback for climate change (Gorham 1991, Bridgman *et al.* 1995, Moore *et al.* 1998). Other greenhouse gases (GHGs) emitted from mires, methane (CH₄) and nitrous oxide (N₂O) are 25 and 298 times stronger GHGs than CO₂ (100-year time span), respectively (IPCC 2007).

The increase of GHGs in the atmosphere is expected to instigate warming in high northern latitudes, especially during winter (Kattenberg *et al.* 1996, IPCC 2007, Moss *et al.* 2010). However, summer temperatures are likewise expected to rise by the end of the century, although not as much as the winter ones (IPCC 2007, Moss *et al.* 2010), possibly causing the seasonal water-table level (WTL) in mires to fall. In pristine peatlands of Finland, it has recently been estimated that climatic warming and drying will decrease total CO₂ sequestration by 41% while increasing total CH₄ emission by 9%, with the greatest changes in CO₂ and CH₄ exchange occurring in fens (Gong *et al.* 2013).

Microbes responsible for heterotrophic soil respiration are sensitive to temperature alterations (Dorrepaal *et al.* 2009). Nevertheless, the sensitivity of soil microbes to temperature is also dependent on soil moisture (Nadelhoffer *et al.* 1991, Moorhead and Reynolds 1993). Hence, a temperature rise alone is not always regarded as a remarkable factor influencing soil carbon balance (Oechel *et al.* 1998). Yet, if soil moisture conditions are favourable for heterotrophic microbes as on mires, the enhancing effect of temperature rise on heterotrophic respiration may be large (Larcher 2003). Dorrepaal *et al.* (2009) reported that a seasonal temperature rise of just 1 °C increased soil heterotrophic respiration in a subarctic fen already by more than 50%. Thus, if all boreal and subarctic mires respond to a 1 °C seasonal temperature rise in the same fashion, even 100 Mt of carbon could be released from mires into the atmosphere (Dorrepaal *et al.* 2009). On the other hand, many recent paleoecological studies on boreal peatlands suggest that warming may also increase plant productivity and therefore carbon sequestration (Charman *et al.* 2013, Loisel and Yu 2013). Further, warmer and drier climate conditions may simultaneously decrease CH₄ fluxes and increase N₂O fluxes from mires (Heymann and Reichstein 2008).

The water-table levels (WTL) in boreal mires are predicted to fall by 14–22 cm due to global warming (Roulet *et al.* 1992). A weak but positive relationship between WTL drawdown and intensified CO₂ emission has been observed in both laboratory and field experiments (Svensson 1980, Moore and Dalva 1993, Bridgham *et al.*

2008, Aurela *et al.* 2009). In the two-year study of Chivers *et al.* (2009), a WTL drawdown of just 5–8 cm significantly decreased net primary production and therefore also the ecosystem's ability to sequester carbon. In their study, WTL drawdown transformed the study site from carbon sink to source already by the second year of monitoring. Furthermore, Riutta *et al.* (2007) found that a WTL drawdown of 14 cm decreased gross photosynthesis 14% but increased ecosystem respiration by 18%, whereas WTL drawdown to 22 cm decreased gross photosynthesis by 22% while increasing ecosystem respiration 20%. In the aforementioned study, heightened ecosystem respiration was primarily attributed to increased peat respiration. However, WTL drawdown has also been reported to increase primary production (Strack *et al.* 2006a, 2006b) and increases in the abundance and productivity of trees are also likely to occur (e.g., Munir *et al.* 2014).

Water-table-level drawdown generally enhances the growth of vascular plants, especially dwarf shrubs, while sedating that of *Sphagnum* mosses (Bubier *et al.* 2007, Riutta *et al.* 2007, Limpens *et al.* 2008). The gradual shift in vegetation alters litter production, accumulation, type and quality, and consequently litter decomposition rates (Dorrepaal *et al.* 2005, Straková *et al.* 2010, 2012). In the short term (several years), net C loss from the soil is likely as the direct effects of drawdown still prevail, e.g., better aeration favouring organic matter decay combined with more or less unchanged quantities of inputs (Straková *et al.* 2010, 2012). During this period, changes in the composition and structure of the plant community are slight. In the long term (decades), however, WTL drawdown spawns dramatic compositional changes in the vegetation community, which may very well offset increased decomposition rates through heightened litter input and accumulation (Straková *et al.* 2010, 2012). Hence, these indirect effects of the environmental change (i.e., drawdown) override the direct ones during long-term hydrosere succession, which means the carbon sink function is not necessarily lost (Straková *et al.* 2010, 2012).

The aim of this study was to quantify the effects of short-term (three years) temperature rise and both short-term (three years) and long-

term (several decades) water-table-level draw-down on momentary fluxes of CO_2 (net ecosystem exchange (NEE) and ecosystem respiration (ER)), CH_4 and N_2O in boreal sedge fens. We hypothesized that warmer and drier conditions will decrease short-term NEE of sedge fens, thus hampering the ability of the sites to function as carbon sinks. Meanwhile, we proposed that the coupling of warming and drying would decrease CH_4 fluxes, but increase those of N_2O . Furthermore, we expect stronger responses in the drainage and warming treatment than in the warming only treatment.

Material and methods

Study sites

The study was carried out on three oligo-mesotrophic sedge fens similar in hydrology. Two of the fens (Lakkasuo, Orivesi and Närhinneva, Virrat) were situated in the middle-boreal coniferous-forest zone ($61^\circ 47' \text{N}$, $24^\circ 18' \text{E}$ and $62^\circ 13' \text{N}$, $23^\circ 23' \text{E}$, respectively), whereas the third (Lompolojänkä, Kittilä) in the northern-boreal zone ($67^\circ 59' \text{N}$, $24^\circ 12' \text{E}$) (Fig. 1). The long-term (1981–2011) mean annual temperature and precipitation were ca. 3.5°C and 700 mm, respectively, and the accumulative temperature sum ($+5^\circ \text{C}$) ca. 1050 degree days for the middle-boreal sites. Correspondingly, the figures for the northern-boreal site were -1.4°C , 511 mm and 700 degree days. Furrow ditches, approximately 20–25 cm deep, for the short-term water-table-level drawdown treatment were dug manually in early May 2008 at the middle-boreal sites and one month later at Lompolojänkä. Drainage operations aimed at long-term water-table-level drawdown were implemented in 1961 at Lakkasuo, 1979 at Närhinneva, and 1972 at Lompolojänkä. Compared with long-term averages, the climate was exceptionally warmer and wetter in 2008 at all three sites (Fig. 2). In 2009, annual temperatures were near average at the mid-boreal sites, which however experienced exceptionally low rainfall that year. The climate at the northern-boreal site was clearly warmer and slightly drier in 2009. In the final study year (2010), both mid-boreal sites were exceptionally cooler than

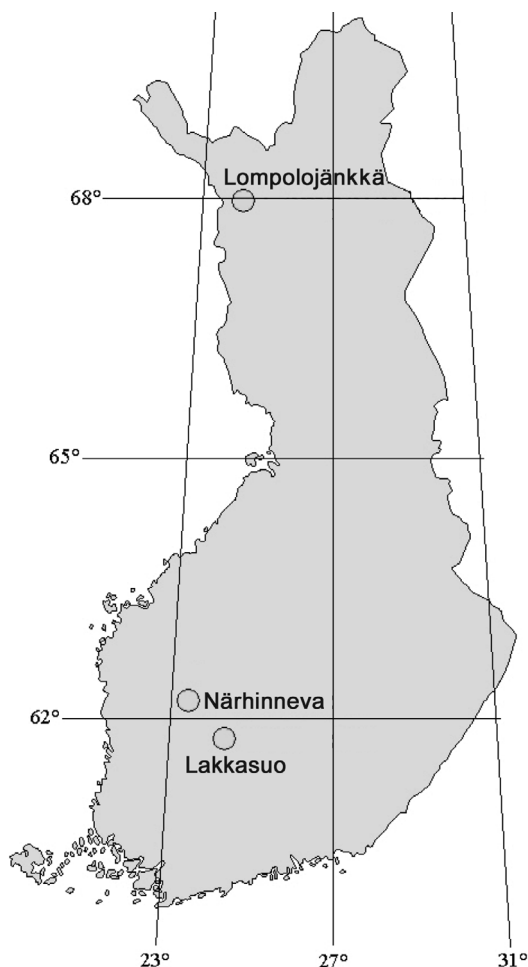


Fig. 1. Locations of the study sites in Finland.

average with the Närhinneva fen also experiencing unusually low rainfall again. The climate at the northernmost site was also considerably drier in 2010, although the air temperature was near average there.

The soil of the sites consisted of *Carex-Sphagnum* peat, ranging in depth from 50 to 200 cm. Lakkasuo harboured the thickest peat layer while Närhinneva the thinnest. The internal variation in peat thickness was greatest at Lompolojänkä, from 50 to 150 cm. In order to provide a general characterization of the vegetation present at the sites studied, coverage was visually estimated as a percentage of plot surface area in two layers, ground (mosses) and field (vascular plants) in late July–early August during the initial season of the study (2008)

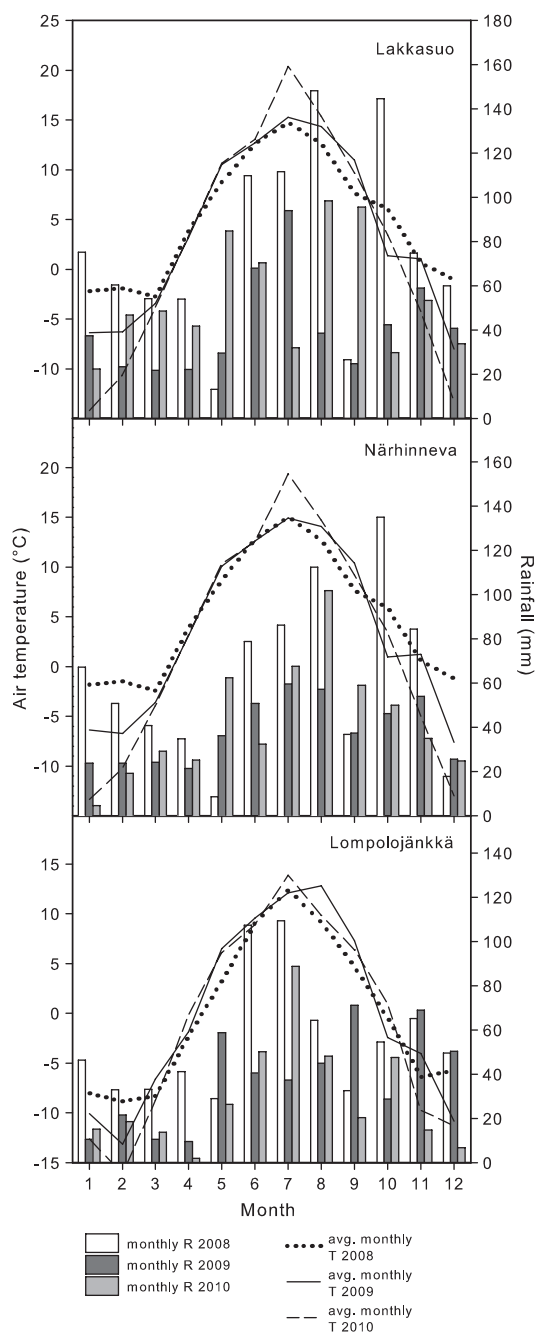


Fig. 2. Average monthly air temperature (T) 2 m above ground and monthly rainfall (R) during the study years (2008–2010) according to site. The data originated from the weather stations in Hyttiälä (for Lakkasuo), Alkkia (Närhinneva), and Kenttäröva (Lompolojänkä) maintained by the Finnish Meteorological Institute. Measured weather data were unavailable for Alkkia (Närhinneva) in 2008 due to station malfunction, thus the data presented have been derived from the 10×10 km weather grid system.

(Table 1). Over the decades, long-term drainage had left its imprint on the vegetation at the middle boreal sites as Scots pine (*Pinus sylvestris*) had become firmly established as a stand with dwarf shrubs and upland forest mosses becoming more common. While the pristine sections of these sites were almost treeless, stand volume in the sections subjected to long-term WTL drawdown had reached $190 \text{ m}^3 \text{ ha}^{-1}$ at Lakkasuo and $55 \text{ m}^3 \text{ ha}^{-1}$ at Närhinneva. At the northern-boreal site, vegetation changes resulting from long-term drainage were rather small as compared with the pristine section, as evidenced by the negligible development of the tree stand, amounting to merely $5 \text{ m}^3 \text{ ha}^{-1}$.

Experimental design

In order to simulate the potential seasonal WTL drawdown scenarios caused by global warming, three 150 m^2 main plots were created at each site: pristine (P), short-term drainage (SD), and long-term drainage (LD). Short-term drainage spanned a period of three years, whilst long-term drainage several decades. Within each main plot, six subplots were established and assigned to one of two warming treatments: control (ambient temperature) and seasonal warming. Thus, the warming treatments were replicated in triplicate in each main plot. To simulate a moderate global warming effect, i.e., a seasonal temperature rise of $0.5\text{--}1^\circ\text{C}$ (see Chivers *et al.* 2009), air and surface soil temperatures were manipulated in the seasonal warming subplots by placing hexagonal open top chambers on them (Chivers *et al.* 2009). The OTCs were constructed from durable transparent polycarbonate and had a projected area of 1.5 m^2 . In order to measure the temperature rise in both soil and air, temperature data loggers (iButton, Maxim, U.S.A.) were placed in each measurement plot 5 cm below and 20 cm above ($T_{\text{air}+20}$) the soil surface. Temperature was monitored at two-hour intervals during the growing season. Eighteen GHG measurement plots were established and organized according to a split-plot design at each site for studying the fluxes of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O). GHG exchange measurements encompassed the interface between the

soil, field and ground layers of vegetation, and air. Due to methodological constraints, tree vegetation was excluded, thus having consequences for the interpretation of ecosystem CO₂ exchange and respiration in the wooded long-term drainage treatments at the middle boreal sites, which are elaborated on in the Results. The simulation of a warming effect using an open top chamber (OTC) did not permit inclusion of entire trees.

In preparation for gas flux measurements, measurement plots were demarcated by first chainsawing the outline of a 60 × 60 cm alumin-

um collar into the ground and thereafter shoving the collar's 30-cm-long sleeve into the trench. This trenching procedure prevented the infiltration, production, and respiration of (new) roots into the delimited area from beyond the bounds of the collar. The superficiality of most of the roots in peatlands (e.g., Finér and Laine 2000) justifies the suitability of the 30 cm trenching depth as a means of accomplishing this. Dying roots within the collar are known to cause a clear CO₂ pulse during the first years after collar insertion (e.g., Minkkinen *et al.* 2007, Mäkiranta *et*

Table 1. Vegetation coverage (percentage of area) according to drainage treatment at the mid-boreal (Lakkasuo and Närhinneva) and northern-boreal (Lompolojännkä) fen sites. All species with coverage $\geq 1\%$ are listed. Coverage determined in late July 2008 at Lakkasuo and Närhinneva, and early August at Lompolojännkä. Abbreviations: P = Pristine, SD = Short-term drainage, LD = Long-term drainage. Each mean is based on species coverage in six subplots per drainage treatment.

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al. 2008), but the effect was regarded as equal in each plot within a given site and treatment. Vegetation inside the collar was not impaired. Boardwalks were constructed around the plots to minimize disturbance to gas fluxes during measurements. Perforated PVC tubes for determining the WTL relative to the soil surface were installed beside the collared plots.

Due to *Sphagnum* growth, the depth of temperature loggers progressively increased over the years. Therefore, we could not vouch for the actual depth in the soil from which continuous temperature measurements were recorded. Further, a portion of the original air temperature data (recorded plotwise and bihourly) from the mid-boreal sites was corrupted during storage. Only sister files containing calculations of daily, treatment-level means could be salvaged in such cases. For these reasons, we rely simply on treatment-level, mean $T_{\text{air}+20}$ in divulging the OTC warming effect in the following.

CO₂ exchange measurement

Prior to gas measurement employing the closed-chamber method (Alm *et al.* 2007), water was poured into the collar groove to ensure an airtight seal of the measurement system upon gas chamber placement. Instantaneous net ecosystem CO₂ exchange (NEE) in each plot was measured with a transparent plastic chamber (60 × 60 × 30 cm) equipped with a fan and a portable infra-red gas analyzer (EGM-4, PP Systems, UK). During a measurement campaign, measurements lasting 90–180 s were conducted under a clear sky (full sunlight) and thereafter under one artificial shade that reduced the amount of incoming light by 40%–60%. All measurements in a campaign were made during a single day. Solar radiation varied no more than 20% between treatment plots or during the measurement period (90–180 s) of a single treatment plot. These precautions were taken in order to ensure as similar conditions as possible for all treatment plots at a site over a campaign. However, the scattered measurement occasions and the use of only one artificial shade did not capture photosynthesis intensities under the lowest levels of solar radiation, in particular. Nevertheless, this was the case

for all treatment plots (and sites); thus, the comparability of treatments was not compromised. During the measurements, CO₂ concentration in the chamber headspace, photosynthetically active radiation (PAR) under the chamber roof, and chamber temperature were recorded at 15-s intervals. After the measurements in light, the transparent chamber was removed and replaced with a metal chamber of the same size and the ecosystem respiration (ER) in the dark was measured. Please note that in the case of the LD treatment at both mid-boreal sites, only *forest-floor* net exchange (NE_{ff}) and respiration (R_{ff}) were measured.

Altogether 16 CO₂ flux measurement campaigns were carried out from late May to late September 2008–2010 at Lakkasuo, and 17 times over the same period at Närhinneva. About 80% of the measurements at both mid-boreal sites were made in June–July. At the northern-boreal site, fluxes were measured 11 times during the period June–September 2008–2010. Although two observations of NEE from each sample plot on every measurement occasion were acquired, some had to be rejected due to irregular (e.g., nonlinear) CO₂ concentration change. After cleaning the data sets, the total numbers of observations of NEE per treatment were 48 at Lakkasuo, 66 at Närhinneva, and 57 at Lompolojänkää. For respiration, the respective numbers were 48, 51, and 33.

Immediately after each gas measurement event, soil temperature at 5 cm depth ($T_{\text{soil-5}}$) was measured to the nearest 0.1 °C from the middle of each plot with a TES-1312A digital thermometer with K type thermocouple input sensor (TES, Taiwan, R.O.C) and stainless steel temperature probe. In conjunction, the WTL to the nearest cm was recorded for each plot by inserting a battery-operated, water sensitive rod into the respective PVC tube and reading the device's metric scale upon hearing a beep. These two variables were measured in order to relate the fluxes to the prevailing environmental conditions.

NEE and ER (NE_{ff} and R_{ff}) were calculated as the linear change in the CO₂ concentration as a function of time by fitting a linear regression line. Positive values of net CO₂ exchange indicate net uptake of CO₂ into the ecosystem (or forest floor) and negative ones net loss of

CO₂ into the atmosphere. Respiration values are stated as negative indicating CO₂ emission, i.e., source.

CH₄ and N₂O flux measurement

CH₄ and N₂O fluxes were determined using the vented static chamber method (Alm *et al.* 2007). For gas sampling, a 30-cm-high metal chamber equipped with a fan and air temperature sensor was set on the collar in the same manner as in CO₂ measurements. Over a 35-minute period, four gas samples were drawn from the chamber headspace via transfer tubes into 35 ml polypropylene syringes after 5, 15, 25, and 35 minutes had elapsed. CH₄ and N₂O concentrations of gas samples were then analysed in the laboratory within 2–3 days using a gas chromatograph equipped with FI and EC detectors. Standards were diluted from a 99.5% solution of CH₄ and N₂O into 600 ml glass bottles. The concentrations used as standards for CH₄ were 8.2 and 82 $\mu\text{l l}^{-1}$, and for N₂O 0.82 and 1.64 $\mu\text{l l}^{-1}$. The gas fluxes were calculated based on the slope of the linear regression between gas concentration and measurement time. All measured fluxes were usable. Positive slopes equated with emission, negative ones consumption. Slightly positive or negative fluxes were common in the data, but zero fluxes were rare. All were included at face value in the data.

Altogether six CH₄/N₂O flux measurement campaigns were carried out during the period June–August 2008–2010 at each of the mid-boreal sites (3 sample plots per treatment \times 6 measurements = 18 observations per treatment). At the northern-boreal site, fluxes were measured seven times during the period June–October 2008–2010 (3 sample plots per treatment \times 7 measurements = 21 observations per treatment).

Statistical analysis

Due to the limited amount of data both annually and overall, we could not reliably model fluxes on which to base simulations of seasonal estimates of carbon balance, CH₄ and N₂O exchange. Therefore, we concentrated on testing

the significance of the drainage and warming effects on instantaneous NEE (NEE_{ff}), ER (R_{ff}), CH₄ and N₂O fluxes separately for each site. In doing so, we sought to verify whether or not OTC warming had a significant impact on fluxes and if any notable interaction with WTL drawdown occurred at the sites.

Since repeated observations were made on the same subjects (i.e., measurement plots) over a period of time (three growing seasons), the observed responses were correlated. As opposed to repeated measures ANOVA, linear mixed models have been designed to handle correlated data with unequal variances from normal distributions (Pan and Connett 2002). Thus, the analyses of instantaneous flux rates were based on fixed effects models with restricted maximum likelihood (REML) estimation method using the linear MIXED procedure in SPSS Statistics ver. 20 (IBM Corp., U.S.A.). Drainage treatment (pristine, short-term WTL drawdown, long-term WTL drawdown), warming treatment (control, OTC), and time were treated as fixed effects. The models defined a split-plot structure with warming as a split-plot treatment. A first-order autoregressive (AR1) covariance structure was assumed for the time correlation. The LSD adjustment method was applied to the confidence intervals and significance values to account for multiple comparisons. A log transformation was performed on the ER data from Lompolojännkä to fulfil normality criteria before applying the fixed effects model. Test results were considered significant at $p < 0.05$.

Results

Impacts on temperature and water-table level

At all sites, the air temperature at 20 cm above the soil surface was principally higher in OTC plots than in control ones (Fig. 3). During the summer months (June–August), $T_{\text{air}+20}$ was on average 0.2 to 2 °C higher in OTC plots. At the mid-boreal sites, the greatest differences in $T_{\text{air}+20}$ occurred within the pristine treatment, while the smallest in the long-term drainage plots (Fig. 3). Shading by the forest stand at both Lakkasuo and

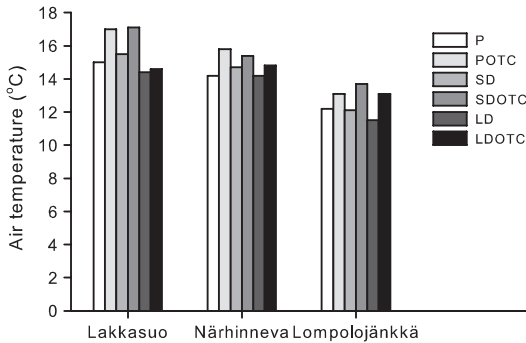


Fig. 3. Mean air temperature at 20 cm above ground according for site, drainage and warming treatments from June through August 2008–2010 based on the bihourly logger data. Abbreviations: P = Pristine (control), POTC = Pristine with open top chamber, SD = Short-term drainage (control), SDOTC = Short-term drainage with open top chamber, LD = Long-term drainage (control), LDOTC = Long-term drainage with open top chamber. Note: Since the time spans covered by logger data varied between sites, only data for the period (June–August) common for all sites was used for calculating the means. Temperature data was unavailable for SDOTC in 2010 at Närhinneva. Temperature data was only available for August in 2008 at Lompolojännkä.

Närhinneva minimised the difference between LD and LDOTC. This was especially evident at Lakkasuo, where stand volume was over three times greater than at Närhinneva. Oppositely, at the cooler northern-boreal site, the differences in $T_{\text{air}+20}$ between OTC and control plots were greatest in both drainage regimes, but smallest in the pristine treatment (Fig. 3). All in all, $T_{\text{air}+20}$ tended to be lowest in plots under long-term drainage regardless of site.

In general, warming of the soil at 5 cm depth was also apparent in response to OTC based on manual measurements made in conjunction with CO_2 flux determination (Fig. 4). However, the differences in $T_{\text{soil-5}}$ were smaller than for $T_{\text{air}+20}$, particularly at Lakkasuo. Unfortunately, these discontinuous measurements of $T_{\text{soil-5}}$ do not adequately account for the inherent temporal variation associated with it. Nonetheless, shading by the forest canopy was also reflected in soil temperature at the middle boreal sites, where long-term drainage accounted for the lowest mean summertime $T_{\text{soil-5}}$.

Short-term and long-term drainage progressively lowered the WTL relative to the pristine

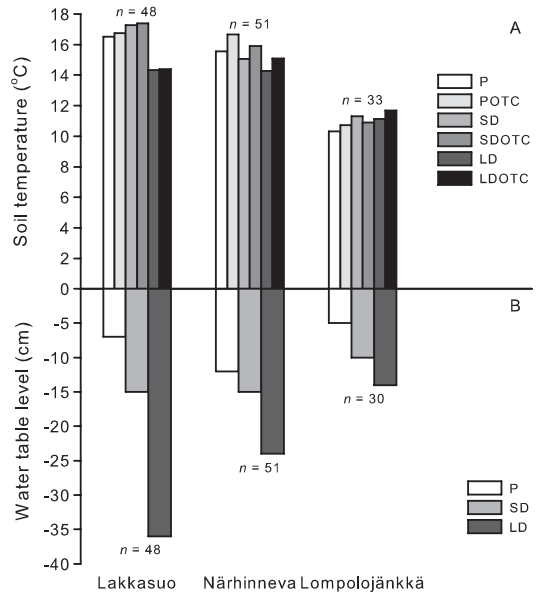


Fig. 4. Mean (A) soil temperature at 5 cm depth and (B) water-table level (WTL, depth below soil surface) by site, drainage and warming treatments. Mean values based on manual measurements made in 2008–2010 in conjunction with CO_2 flux determination. Abbreviations: P = Pristine (control), POTC = Pristine with open top chamber, SD = Short-term drainage (control), SDOTC = Short-term drainage with open top chamber, LD = Long-term drainage (control), LDOTC = Long-term drainage with open top chamber. The n values above or below the bars are numbers of observations.

treatment at all sites, but these effects were most pronounced at Lakkasuo (Fig. 4). Short-term drawdown lowered the WTL the least at Närhinneva, whereas long-term drawdown did so at Lompolojännkä. The highest mean WTLs for all treatments occurred namely at the northern-boreal site, all lying within 9 cm of each other. Hence, this fen was the wettest of all the sites.

Net CO_2 Exchange

While the main effects of drainage treatment and OTC warming were both significant at Lakkasuo, only drainage had a significant effect at the other mid-boreal site, Närhinneva (Table 2). Contrary to the mid-boreal sites, neither WTL drawdown nor warming influenced NEE at the northern-boreal site.

At Lakkasuo, where the mean WTLs under the pristine, short-term, and long-term drainage

regimes contrasted most sharply, drainage progressively and significantly reduced NEE (and NE_{ff}) relative to the pristine treatment (Fig. 5). In addition, NE_{ff} in the long-term drainage treatment was significantly lower than NEE in the short-term WTL drawdown treatment. Just like drainage, OTC warming also diminished the rate of NEE (and NE_{ff}) overall as compared with the values for the control plots at Lakkasuo; this trend was evident specifically under both WTL drawdown regimes there, although interaction between the drainage and warming effects was not significant (Table 2 and Fig. 5).

At Närhinneva, only the decreasing effect of long-term WTL drawdown on NE_{ff} was apparent, which led to significantly lower rates with respect to NEE of the other treatments (Fig. 5). As opposed to those in Lakkasuo, the WTLs in the pristine and short-term drainage treatments at Närhinneva differed little, which likely contributed to the similarity in NEE between the two. Admittedly, the drop in the WTL resulting from the short-term drainage procedure failed to meet expectations as the plots remained wetter than desired. At the northern-boreal site, Lompolojänkä, the distinctly similar NEEs between treatments were rather expected considering that the mean WTLs lay within close range of each other

as well as being the highest of all sites (Figs. 4 and 5). In contrast to Närhinneva, however, the limited WTL drawdown achieved via both drainage regimes at Lompolojänkä was purely a consequence of climatic factors. Despite comprehensively warmer air temperatures at 20 cm above ground with OTC than without at all three fen sites (Fig. 4), the achieved warming was of no perceivable consequence for NEE (or NE_{ff}) at two of them, Närhinneva and Lompolojänkä.

Respiration

The trends present in net CO_2 exchange were mostly reiterated in respiration (Table 2 and Fig. 5). Only long-term drainage significantly increased (forest floor) respiration at the middle boreal sites, which consequently exceeded ER rates in the other treatments (Fig. 5). R_{ff} excludes tree crown respiration, thus ecosystem-level respiration for LD/LDOTC at these two sites would naturally be higher (i.e., more negative). At Lompolojänkä, as with NEE, ER rates were likewise similar in all treatments.

No effect of OTC warming on respiration was found, thus the presence of OTC did not alter CO_2 emission from pristine, short-term or

Table 2. Results of the sitewise fixed effects models for net CO_2 exchange, respiration, CH_4 and N_2O fluxes. D = drainage treatment (pristine, short-term drainage, long-term drainage), W = warming treatment (control, open top chamber). D and W represent main effects and D \times W their interaction. An effect was deemed significant if $p < 0.05$.

Independent variable	df	Lakkasuo		Närhinneva		Lompolojänkkä	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Net CO₂ exchange							
D	2	369.31	< 0.001	69.36	< 0.001	1.01	0.390
W	1	4.47	0.047	0.01	0.917	1.56	0.232
D × W	2	2.43	0.112	0.22	0.805	0.43	0.662
Respiration							
D	2	13.33	0.001	9.52	0.003	0.70	0.515
W	1	0.07	0.791	0.22	0.647	1.22	0.290
D × W	2	0.96	0.407	0.21	0.817	0.06	0.941
CH₄ flux							
D	2	14.10	< 0.001	39.39	< 0.001	221.02	< 0.001
W	1	1.02	0.330	0.33	0.573	1.55	0.226
D × W	2	0.49	0.623	0.10	0.910	1.15	0.337
N₂O flux							
D	2	2.86	0.082	5.99	0.011	0.25	0.781
W	1	0.84	0.372	0.08	0.784	0.60	0.452
D × W	2	0.53	0.598	1.35	0.285	0.29	0.756

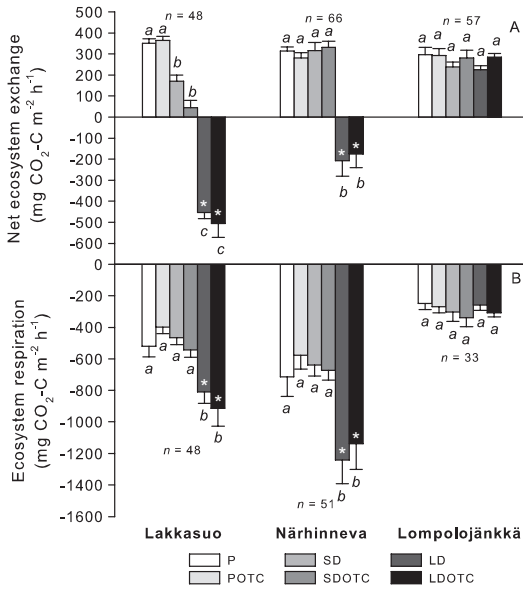


Fig. 5. Mean (A) instantaneous net CO_2 exchange and (B) respiration rates by site, drainage and warming treatments during the growing season 2008–2010. Positive net ecosystem exchange (NEE) values indicate carbon sink and negative ones source; negative ecosystem respiration (ER) values indicate CO_2 emission; however, net exchange and respiration rates for LD/LDOTC at the mid-boreal sites (Lakkasuo and Närhinneva) are only representative of the forest floor (NE_f , R_f) since the tree stand has not been considered in the calculations (the bars indicated with asterisks). The LD/LDOTC treatment plots were almost treeless at the northern-boreal site (Lompolojankkä). Different lowercase letters above or below the bars indicate significant (at $p < 0.05$) differences between corresponding treatments at each site. The total numbers of observations (n) are given above or below the bars. Error bars indicate standard error of the mean. Abbreviations as in Fig. 4.

long-term drainage plots anywhere (Table 2 and Fig. 5). While a similar magnitude of NEE was shared by all sites, ecosystem respiration was clearly lower at the northern-boreal site as compared with that at the mid-boreal ones.

CH₄ flux

With respect to the pristine treatment, short-term WTL drawdown decreased methane emissions significantly at Lakkasuo and Lompolojankkä (Table 2 and Fig. 6). Long-term WTL drawdown suppressed the release of CH_4 most of all, and the significance of this effect could be detected

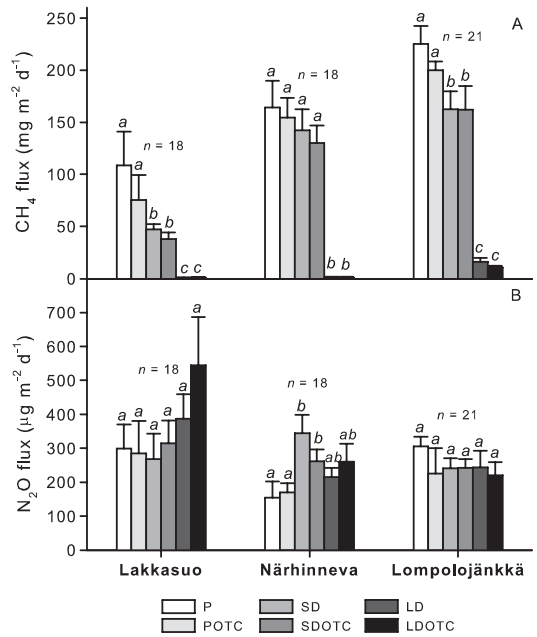


Fig. 6. Mean (A) instantaneous methane and (B) nitrous oxide flux rates by site, drainage and warming treatments during the growing season 2008–2010. Positive values indicate emission. Abbreviations as in Fig. 4. Different lowercase letters above or below the bars indicate significant (at $p < 0.05$) differences between corresponding treatments at each site. The total numbers of observations (n) are given above the bars. Error bars indicate standard error of the mean.

at all three sites. Once again, OTC warming as such or coupled with drainage brought forth no apparent consequences on CH_4 fluxes anywhere.

Although NEE and ER were not affected by WTL drawdown at the northern-boreal site, the drop in the WTL under both drainage regimes sufficed to significantly reduce CH_4 emissions there. At Närhinneva, however, the short-term WTL drawdown achieved was insufficient to alter CH_4 fluxes in addition to NEE and RE. Furthermore, when considering the magnitude of fluxes amongst the three sites, the lowest mean CH_4 emissions occurred at Lakkasuo and the highest at Lompolojankkä, and this applied to all treatments.

N₂O flux

At the mid-boreal sites, WTL drawdown generally tended to increase nitrous oxide emissions

relative to the pristine treatment, but such was not the case for the northern-boreal site (Fig. 6). However, significant differences between treatment differences were found only at Närhinneva, where short-term drainage increased N_2O emission most clearly (Table 2 and Fig. 6). All sites and treatments considered, the impact of OTC warming on N_2O fluxes was indiscernible. The long-term drainage treatment at the mid-boreal site, Lakkasuo, accounted for the highest mean N_2O emissions.

Discussion

The degree of warming achieved via temperature manipulation using OTCs and the difference in average WTLs between the pristine and short-term drainage treatments in this study were close to those presented by Chivers *et al.* (2009). In addition, the increases in air and soil temperatures caused by OTCs here corresponded with the results of Munir and Strack (2014), although here we did not statistically test the differences in air or soil temperatures. In general, instantaneous rates of NEE and ER (and NE_{ff} and R_{ff}) in our study roughly corresponded to those measured in earlier studies on pristine and drained peatland sites (Frolking *et al.* 2002, Riutta *et al.* 2007, Aurela *et al.* 2009, Chivers *et al.* 2009, Drewer *et al.* 2010, Ojanen *et al.* 2010, Badorek *et al.* 2011). In our data, the impacts of long-term drainage stood out from those initiated by short-term drainage or OTC warming. (1) OTC warming had little effect on CO_2 fluxes and no effect on CH_4 or N_2O fluxes. (2) No drainage effects were observed in the northernmost and wettest site except on CH_4 fluxes. (3) A more straightforward effect of drainage decreasing CH_4 emissions was apparent. Since the carbon exchange and respiration results for the long-term drainage treatment at the mid-boreal sites do not apply to the whole ecosystem, rather just the forest floor, they will be dealt with separately here.

Lakkasuo was the only site where ecosystem CO_2 fluxes were notably affected by short-term WTL drawdown and warming. Short-term drainage decreased NEE, which coincides with the findings of Riutta *et al.* (2007) from the same site as well as Chivers *et al.* (2009) from an Alaskan

rich fen. However, ecosystem respiration in our study remained unchanged, which conflicts with the heightened ER found by Riutta *et al.* (2007) as well as by Ballantyne *et al.* (2013) in a poor fen in northern Michigan. The latter-mentioned study reported no significant change in NEE, though. Similar to our results, Chivers *et al.* (2009) found no difference in ER between control and lowered water table treatments. They attributed this phenomenon to reduced plant C uptake (and thus plant growth), suggesting that autotrophic respiration declined while heterotrophic respiration rose, thereby offsetting any change in ER. The significant overall effect of warming on NEE found at Lakkasuo, in turn, conflicted with the results of Chivers *et al.* (2009). In their study, proportionally similar increases (16%) in both gross photosynthesis and ER overall due to warming were observed, therefore NEE was unaltered; here, on the other hand, warming at Lakkasuo caused a notable reduction in NEE overall because gross photosynthesis decreased while ER continued steadfastly. Our results from Lakkasuo thus seem to demonstrate that the combined influence of short-term WTL drawdown and warming had unfavourably altered the growing conditions of the vegetation community present hence forcing it into an adjustment phase, as evidenced by lowered NEE (and gross photosynthesis). Although we cannot attest to any changes in community composition and structure as we did not monitor them in this experiment, functional disruption to the community had evidently occurred. Gradually, dwarf shrubs would benefit from the drier environment becoming more abundant (Riutta *et al.* 2007, Badorek *et al.* 2011), but given the brief time scale of our study, their influence on CO_2 fluxes would have been minor. On a poor fen, Strack and Waddington (2007) found no significant difference in CO_2 exchange after short-term WTL drawdown relative to the control, but demonstrated differential responses of carbon cycling to drawdown between microforms (hummocks, lawns, hollows). They also emphasized that the vegetation communities inhabiting different microforms were still undergoing change, which means their full response had yet to be determined.

The small change in the WTL resulting from short-term drainage largely accounted for the

lack of differences in NEE and ER at the other mid-boreal site (Närhinneva), and high moisture levels proceeded to reduce temperature sensitivity of C fluxes as has been documented in a number of studies (e.g., Moore and Dalva 1993, Mäkiranta *et al.* 2010, Pearson *et al.* 2012). Our northern-boreal site, on the other hand, highlighted how geographical location and climate can dictate the response of ecosystem CO₂ fluxes to environmental change, i.e., altered hydrology and temperature do not necessarily affect boreal fens in the same way. In contradiction with the findings of Oechel *et al.* (1998) from wet sedge tundra ecosystems, CO₂ fluxes at Lompolojänkää were insensitive to both drainage and warming with no indication of any interaction. In Oechel *et al.* (1998), principally drainage, but also elevated temperature, intensified particularly ER. The divergence of our results becomes even more intriguing when considering the difference in the thickness of the organic soil layer: 50–150 cm in this study, and 15–30 cm in Oechel *et al.* (1998). Although we must exercise restraint in our interpretation due to the limited size of our dataset, obviously the high water-table levels in both the short-term as well as long-term drainage plots kept ER in check at Lompolojänkää by limiting the thickness of the aerobic soil layer and thus decomposition (Strack *et al.* 2006b). We suspect that these results may also be related to Lompolojänkää's methane budget. Previously, Drewer *et al.* (2010) identified methane as the dominant GHG there. In our study, methane emissions continued at a rather high level despite drainage (Fig. 6), which indicates the continued release of organic material into the anaerobic peat layers and consequent anaerobic respiration of microbes in addition to CH₄ transport through the root-shoot pathway. Moreover, this ecosystem has been characterized as highly N limited (Lohila *et al.* 2010), which sets restrictions on plant growth, while potentially hampering the activity of methanotrophs (Bodelier and Laanbroek 2004). In any case, CO₂ fluxes remained stable over the short term at this high-latitude fen, with the climate there seemingly acting as a buffer against drastic environmental change.

As described in Material and methods, the net CO₂ exchange measured in the long-term drainage treatments at both mid-boreal sites is

only representative of non-tree vegetation on the forest floor. This explains the net losses of carbon from LD/LDOTC as seen in Fig. 5; as both sites are wooded, carbon is also stored in tree stems in addition to accumulating in soil via above and belowground tree litter input, but this has been ignored here. Furthermore, R_{ff} measured (which consequently affects NE_{ff}) includes decomposition of fallen tree needles and leaves, as these were not removed from the plots during the study, as well as tree root litter at least at the start. These forested sites should not however be erroneously interpreted as carbon sources. While this methodological handicap obviously hinders interpretation of the effects of LD/LDOTC on ecosystem carbon fluxes, incorporating the forest stand into the experimental framework and calculations is far from straightforward. In any case, the contributions of these above-mentioned factors to the NE_{ff} and R_{ff} rates registered would presumably be the same in both LD and LDOTC plots. At the northern-boreal site, on the other hand, no such interpretational quandary exists since long-term WTL drawdown had had a negligible effect on tree establishment and growth there, remaining almost treeless.

Based on our instantaneous measurements, the forest floor typically constituted a source of CO₂ to the atmosphere because photosynthesis of the ground vegetation was surpassed by respiration from autotrophic (ground vegetation and some tree roots) and heterotrophic sources (i.e., decomposition of litter and peat). In one of the few studies examining the role and contribution of forest floor vegetation in peatland forest C dynamics, Badorek *et al.* (2011) made the same observation in a nutrient-poor, forestry-drained peatland site in southern Finland. Furthermore, they reported that the forest floor was responsible for 20%–30% of all the CO₂ assimilated by the forest ecosystem. In comparison, the coverage of mosses and dwarf shrubs in the plots subjected to long-term WTL drawdown at our mid-boreal sites was considerably smaller, especially at Lakkasuo, than in Badorek *et al.* (2011), thus in our case the forest floor would likely account for a lower proportion of the C sequestered by the whole ecosystem. Despite similar species of vegetation as in the site studied by Badorek *et al.* (2011), Lakkasuo and Närhinneva were some-

what richer sites, which in part may explain why instantaneous rates of forest floor respiration were also several times greater. Moreover, forest floor vegetation occurred in patches at Lakkasuo due to shading by the forest canopy, while being continuous in the better lighted conditions at Närhinneva. As a result, measured rates of NE_{ff} were nearly always negative (i.e., net release of CO_2) in the long-term drainage plots at Lakkasuo, but positive rates (i.e., net uptake of CO_2) were not uncommon at Närhinneva. Just as Badorek *et al.* (2011) surmised, since litter input was overlooked and some degree of tree root respiration (and root litter decomposition) is included in these CO_2 exchange measurements, the results presented plausibly overestimate respiration and underestimate photosynthesis of the forest floor. Indeed, a number of methodological challenges exist in estimating the carbon fluxes of wooded forestry-drained peatland sites in response to simulated warming and water-table-level drawdown. Ideally, any simulated warming should also target the tree crown, instead of just root systems. Further, the OTC treatment we applied was only short in duration, as opposed to drainage in the long term which had already spanned decades.

Mean daily methane fluxes at the mid-boreal sites were in line with those found by Nykänen *et al.* (1998), and those for Lompolojänkka agreed with the findings of Huttunen *et al.* (2003) and Drewer *et al.* (2010). As has been noted in numerous previous studies on peatlands (e.g., Roulet *et al.* 1992, Nykänen *et al.* 1998, Turetsky *et al.* 2008, Ojanen *et al.* 2010), drainage curtailed methane emissions considerably at all three of our sites. Although peat temperature positively correlates with CH_4 emission (Bubier *et al.* 1995, Nykänen *et al.* 1998, Huttunen *et al.* 2003), simulated warming with OTC produced no discernible impact on fluxes anywhere. However, it is unclear as to whether the warming treatment applied here, which was not only short in duration (three years) but limited in extent (i.e., each OTC covering an area of 1.5 m²), would have affected soil temperature lower down in the peat profile; for instance, using the same methodology Chivers *et al.* (2009) perceived no influence on soil temperature below 2 cm from the soil surface. On the other hand, in examining

the effects of WTL drawdown and warming on CH_4 fluxes in a dry boreal bog, Munir and Strack (2014) found that OTCs significantly warmed air temperatures as well as soil temperatures at 5 cm while also noting an effect, though not significant, on temperatures to 30 cm depth. However, they still found no significant effect of OTCs on CH_4 emissions. Furthermore, only small increases in CH_4 emissions resulted from soil warming in the WTL drawdown treatment on a rich fen in the study by Turetsky *et al.* (2008). Similarly, soil warming did not affect CH_4 fluxes in fen mesocosms, while WTL clearly acted as the dominant control (White *et al.* 2008). Nevertheless, White *et al.* (2008) noted major indirect effects of warming and WTL on pore water chemistry and plant productivity, which were deemed important secondary factors in explaining CH_4 fluxes. In congruence with Huttunen *et al.* (2003), CH_4 emissions in our study were higher from the northern-boreal site than its mid-boreal counterparts apparently due to both high levels of moisture and fertility.

N_2O emissions from pristine peatlands are generally low (Regina *et al.* 1996, Song *et al.* 2009, Drewer *et al.* 2010, Lohila *et al.* 2010) and our study likewise confirms this. N_2O fluxes in the pristine treatment at all sites were well within the range measured by Lohila *et al.* (2010) and Drewer *et al.* (2010), but flux rates at Lakkasuo and Närhinneva exceeded those of both Nykänen *et al.* (1995) and Regina *et al.* (1996) from middle boreal fens. WTL drawdown typically leads to increased emission of N_2O in minerotrophic peatland sites (Regina *et al.* 1996, Ojanen *et al.* 2010) and this could also be witnessed here at both mid-boreal sites. Although the slight lowering of the water table over the short term at Närhinneva generated no noticeable effect on CO_2 or CH_4 fluxes, it nonetheless increased the release of N_2O by almost twofold compared to the pristine state. This would appear to indicate increased mineralization and nitrification of the N pool wrapped up in the organic matter, hence providing nitrate for denitrification and enhanced N_2O emission (Maljanen *et al.* 2012). Since we did not partition OM decomposition from ecosystem respiration, we cannot verify its specific impact on CO_2 emission, but ER nonetheless remained unchanged. The lower

N_2O emissions of the pristine treatment could be due to either the low availability of nitrate and/or reduction of N_2O to N_2 caused by greater soil moisture (higher WTL) and consequently low oxygen availability (Lohila *et al.* 2010, Maljanen *et al.* 2012). The margin between production and consumption of N_2O in soil is not absolute, for the processes of nitrification and denitrification may occur in thin, abutting layers of soil (Flechard *et al.* 2005, Pihlatie *et al.* 2007, Lohila *et al.* 2010). Thus, even though the drop in the WTL was ostensibly small under the short-term drainage regime, it may have been significant from the aspect of microbes involved in these processes. Furthermore, the topmost organic soil layer, which is the recipient of incoming N via atmospheric deposition or organic matter decomposition, is known to be crucial in the soil–atmosphere exchange of N_2O (Regina *et al.* 1998, Pihlatie *et al.* 2007, Lohila *et al.* 2010). Additionally, soil acidity possibly accounts for some of the observed enhancement of N_2O emission; the oligotrophic Närhinneva fen represented the poorest of our three sites, purportedly having a lower pH. Previously, acidic soil has been associated with the highest N_2O emissions in a Swedish forestry-drained peatland (Andert *et al.* 2012). During denitrification, soil pH has likewise been demonstrated to negatively correlate with $\text{N}_2\text{O}:\text{N}_2$ product ratios (Simek and Cooper 2002, Dannenmann *et al.* 2008). On the contrary, Macrae *et al.* (2013) suggested that soil water retention above the water table following drawdown (up to 20 cm) limits the effects of drainage on microbial activity and nutrient cycling because the soil moisture content remains largely unchanged.

Just as with CO_2 fluxes, N_2O fluxes at our northern-boreal site, Lompolojänkka, did not respond to WTL drawdown or warming. Since the change in the WTL after drainage remained small, we suppose that oxygen availability in the peat was not affected enough to alter the N cycle.

Previously at this nutrient-rich sedge fen, Lohila *et al.* (2010) attributed the relatively low N_2O fluxes to the low nitrate concentration of the peat and high water-table level. The former restricts microbial denitrification, while the latter creates an anaerobic soil environment which leads to a shift in the end product of denitrifica-

tion from N_2O to N_2 as N_2O is used by microbes in the absence of oxygen (Davidson *et al.* 2000, Lohila *et al.* 2010). Furthermore, in their analysis Lohila *et al.* (2010) found that the peat consumed N_2O at a depth of 15 cm. Although a considerable amount of organic N is stored in the peat at Lompolojänkka, atmospheric N deposition is low and mineralized nitrogen scarce (Drewer *et al.* 2010, Lohila *et al.* 2010). All of these factors probably contributed to the lack of effects on N_2O dynamics we observed there.

Conclusions

If we reflect on our hypotheses, we find that our study provided rather modest evidence to support them. All sites and gases considered, the impact of simulated warming was for the most part neutral, the only exception being one of the two mid-boreal sites, where warmer and drier conditions caused NEE to decrease. Otherwise, the temperature rise alone or coupled with WTL drawdown did not alter CO_2 , CH_4 or N_2O fluxes at the mid-boreal or northern-boreal sites. Instead, the drainage effect seemed to override that of simulated warming. Primarily WTL drawdown accounted for the differences in fluxes detected, but this was more apparent at the mid-boreal sites than our northern-boreal one. In fact, the northernmost Lompolojänkka sedge fen was least sensitive to temperature rise and drainage; there, we could only attest to the curbing of CH_4 emissions in response to WTL drawdown. As controls of microbial processes, the cooler and wetter conditions and N limitation at this site appeared to buffer it against environmental change — warming and drying — over the short term. However, due to the limitations of our dataset, this study serves chiefly as a stepping stone to intensive, future studies on the subject which should consider, e.g., the annual C balance, long-term influence on fluxes, and tree stand component (on forested sites).

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